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A VEGETATIVE MUTANT, AND THE PRINCIPLE OF HOMOEOSIS IN PLANTS

CONTRIBUTIONS FROM THE AMES BOTANICAL LABORATORY, NO. 9

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(WITH NINETEEN FIGURES)

When viewed in their relations to morphogenetic and broader evolutional problems (as distinguished from narrower phylogenetic, or genealogic, problems) numerous facts of teratology—a descriptive cult without unifying principles, heretofore pursued chiefly by the vaguely curious, and lending itself discreditably with equal readiness to either side of many a morphological discussion in the past—manifest a special and high value. The production of form from formlessness in the egg-derived individual, the multiplication of parts and the orderly creation of diversity among them, is an actual evolution, of which anyone may ascertain the facts, but of which no one has dissipated the mystery in any significant measure. This micro-evolution forms an integral part of the grand evolution problem and lies at the base of it, so that we shall have to understand the minor process before we can thoroughly comprehend the more general one. Morphogenetics, therefore, is a field in which the evolutionists must work. The development, or morphogenesis, of a single individual—if it be such a case as may improve our insight into the nature of the ontogenetic process micromechanically considered—may be of as great interest in the eyes of the evolutionist as the origin of a new race or the fate of an old one.

It is this relation, to the central rather than the peripheral problems of evolution, which has led me to carry out certain observations upon abnormalities in plants. Yet I shall try to make clear, also, the bearing which some of the observed individual variations have upon types of racial variation. In this connection some facts of normal, i. e., established, morphology will be noticed. The main principle under discussion seems to deserve a place, though a minor one, in any complete account of the evolution of species.

The present paper is sequel to a casual observation made several years ago, when as I was passing near a horsechestnut tree in the autumn I noticed, upon a depending branch, a leaf which had lost several of its leaflets. I found that the palmately compounded leaves of this species fall to pieces as they are cast off by the tree, or even before this event. The leaflets are removed as if by a clean cut; and sometimes the petiole, quite devoid of blades, is left standing alone upon the stem.

This complete dismemberment seemed to me a curious thing. Abscission at the base of the petiole is not a simple decay, but is, as everyone knows, a somewhat complicated process, wherein there is formed across the leaf-stalk, through suitable cell divisions, a plate or layer of cells, by the disintegration of which the leaf is ultimately allowed to fall away. The cell walls of the scar-surface become suberized, so that the wound is sealed against the loss of water. Leaf-abjection is thus a complex adaptive process.

The question arose, Why should the abscission proper to the petiole-foot be repeated in all of its details at the bases of the petiolules?—for I ascertained that the process is carried out in full at these points in this species. Of what use to the tree is it that the frame of the leaf, now emptied of its valuable contents which have been withdrawn into the stem, should be carefully disarticulated? I have never been able to imagine any utility nor have those to whom I have propounded the riddle suggested any. I believe that in fact the habit is neutral in the tree's economy.

If this is so, the evolution of absciss-layers in petiolules cannot be referred to natural selection. For in the plan of evolution by the accumulation of variations under the guidance of natural selection, developing organs must pay their way as they go.

An explanation of the presence of the useless structures occurred to me. It seemed probable that the absciss-layer perfected in the natural course of evolution at the foot of the leaf-stalk had, subsequently to the compounding of the blade in this species, been transferred, so to speak, to the bases of the petiolules. The disarticulations of the leaflets seemed to be a series of ecologically meaningless echoes of the primal, useful disarticulation at the junction of stem and petiole.

The horsechestnut is not peculiar in this respect, and further considerations, with regard to compound leaves generally, have confirmed in my own mind my first understanding of the matter. Disarticulation of the leaflets seems to be universal in deciduous-leaved species. It occurs in many families separated in a natural system by entire-leaved groups, as in Juglandaceae, Berberidaceae, Anonaceae, Rosaceae, Rutaceae, Sapindaceae, Vitaceae, Oleaceae, Bignoniaceae, Caprifoliaceae. That is, it must have arisen in evolution many times independently. There must, then, be some wide underlying principle capable of bringing the disarticulation in question to light, wherever compounding of the blade establishes the conditions for its operation. This principle seems, as has been argued above, not to be natural selection. There is, however, in plants a recognizable principle of morphic translocation, mobility of characters, or *homoeosis* (BATESON), to which the phenomenon may very well be referred.[1] The conditions favorable to its operation in this case are very obvious, since the structural relations at the junction of the petiole and stem are imitated at the junction of petiolule and petiole (or rhachis).

The Pierson fern

Recently evidence corroborating the above interpretation has come to hand in a case where advance in complexity has been all but observed. In the title I have alluded to it as a case of mutation; but perhaps I am using the word somewhat loosely, if the DeVriesian sense is to be insisted upon. The plant is the Pierson fern, now well known to horticulturalists and to the public generally. The metamorphosis of the Boston fern, to which the Pierson owes its origin, seems not to have been hitherto described as a homoeotic transformation; yet such it is.

The first plant of the variety was found while it was still small, among vegetatively propagating Boston ferns in the greenhouses of Mr. F. R. PIERSON, the well-known horticulturalist of Tarrytown-on-Hudson, N. Y., in 1900.[2] While it was not a "pedigreed" plant, its derivation is patent, for when its descendants are grown under poor conditions, they generally revert temporarily, in a part of their fronds at least, into the primitive state, which is seen to be that of the Boston fern. This constitutes highly desirable proof of parentage. Whether the sudden alteration of character took place in a spore, or in a bud from a runner, is not surely known. Nevertheless the circumstances leave little doubt on this head; for the Boston fern, while richly stoloniferous, is almost universally sterile. Mr. PIERSON believes the original individual to have been a bud-sport. The young plant caught the eye of a gardener, who brought it to the notice of Mr. PIERSON, and it was set aside so that its development might be followed. All Pierson ferns and numerous varieties have descended from this individual.

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[1] My first paper on this topic, entitled "On translocation of characters in plants," appeared in Rhodora 7:14–19, 21–31. 1905. When it was written I did not know that BATESON had briefly treated the same subject in relation to variation of animals and had devised the name homoeosis. I find his term applicable to the present purpose and more convenient to use than my own expression.

[2] Mr. F. R. PIERSON, in a letter to the writer.

In this case we may say that the transformation, which affects the leaves of the fern and consists not in the introduction of altogether novel outlines or proportions, but rather in the relocation of forms already in existence, has taken place under observation. A single individual has been noted to emerge from the common mass—under cultivation as an isolated colony—with very markedly altered characters. New features have not been slowly developed through several generations, but have appeared suddenly.

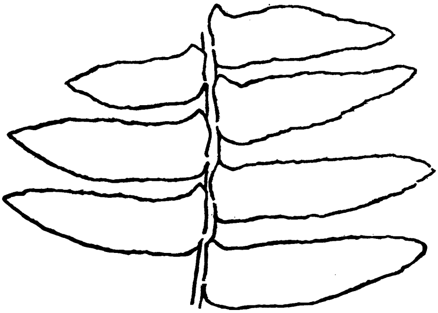

FIG. 1.—Pinna of Boston fern.

The Boston fern has simply pinnate fronds. The pinnae are entire, serrulate-margined, oblong, and usually bluntly toothed or auriculate on the upper margin at base (*fig. 1*). In the new plant, the pinnae have become divided,[3] and at the same time elongated—often much elongated. Their divisions, the pinnules, are oblong and, when fully developed, toothed or auriculate on the upper margin at base (*fig. 2*). The pinnules, in fact, are very good copies of the

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[3] When the new form is fully expressed. The division may affect only part of each pinna.

original pinnae; and if we lay a well-developed pinna of the Pierson fern by the side of a small frond of the Boston fern, we shall be struck with the fact that they are almost identical. In short, the pinnae of the new variety are transformed from the original condition in such a way that the plan of the whole frond of the Boston fern is now seen in the primary segments of the Pierson frond.

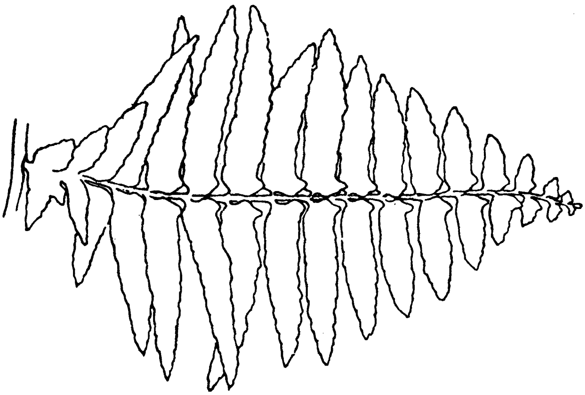

FIG. 2.—Pinna of Pierson fern.

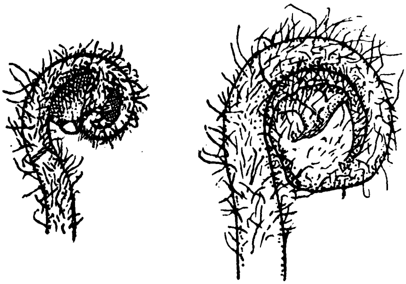

FIG. 3.—Growing apex of pinna of Pierson fern (left) and Boston fern (right).

The completeness of the imitation may be indicated still further:

1. The pinnae are elongated, the growth being less strictly determinate than that of the original pinnae, and more like that of the frond.

2. The apical growth of the pinnae is now circinnate, as shown in *fig. 3*, after the fashion of the original frond. The pinnae of the Boston fern on the other hand, while lapped together in the young state at the summit of the developing frond, are not in the least circinnate.

3. The blades of the pinnae are divided.

4. The outline of the pinnules is like that of the original pinnae.

5. Finally, the peculiarity of the original form, that its pinnae in age become disarticulated by the development of an absciss-layer,

and ultimately fall off after several layers of brown tissue have been developed on the scar surface-to-be, is now shown by the pinnules of the Pierson fern. The pinnules of the latter are discovered to be deciduous, and a minute investigation shows that deciduity is secured by the development of an absciss-layer at the base of the pinnule, with the formation of brown scar-tissue. Thus the translocation of the structures concerned in disarticulation of leaflets is in this case an ascertained occurrence: these structures have passed at once and unaltered from the bases of the pinnae to the bases of the pinnules.

The beautifully soft and luxuriant aspect of such ferns as the Whitman[4] is due to the fact that each frond is in effect made up of many small fronds. In this last-named variety, and in some others, as Pierson's *elegantissima* and *superbissima*, homoeosis has gone one step farther than in the Pierson, so that we find a thrice-compounded leaf (*fig. 4*), and the segments of the third order have the frondlike character—even to the circinnate apical growth.

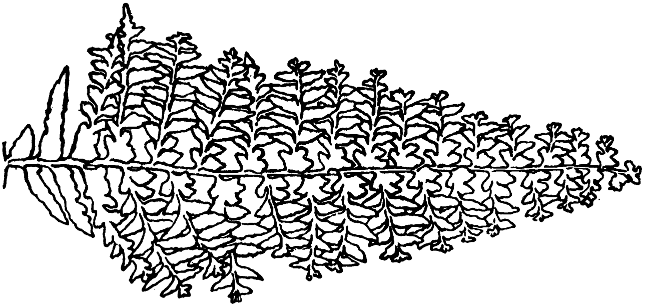

FIG. 4.—Pinna of Whitman fern.

To return to the matter of normal casting of leaflets, with which we began. The fact that in an instance now before us positive evidence of the translocation of absciss-layers, etc., from one part of the leaf to another has been secured, strongly corroborates the inference already made on more speculative grounds, that leaflet-abjection in general is to be understood as an imitative or repetitive phenomenon.

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[4] The Whitman fern originated in the greenhouse of H. H. BARROWS & SON, Whitman, Mass., in 1904, as a bud-sport, upon a runner of the Barrows fern (itself a sport from the Pierson).—Letter from H. H. BARROWS & SON to the writer.

The principle of homoeosis

But whether or not the transference of absciss-layer from leaf to leaflets in this fern verifies in any material degree the idea of a translocational origin for leaflet-abjection, it alone, were there no other available demonstration, would suffice to establish the important truth, that a character perfected in the course of evolution under one relation in the plant body may make its appearance suddenly under another relation and in a region of the body to which it is not native. Here is a principle of wide import in morphogenesis, and not without bearing—as has just been shown—upon some of the minor problems of plant evolution; concerning which principle some further observations may be offered.

The described involution of frond-plan belongs to one among several categories of homoeosis all subsumed under the larger type, but of this type it is a rather complicated example. A simpler illustration will make the nature of the general principle clearer, and at the same time exhibit its distinctness from another aspect of morphogenesis with which it is frequently confused—that of reversion.

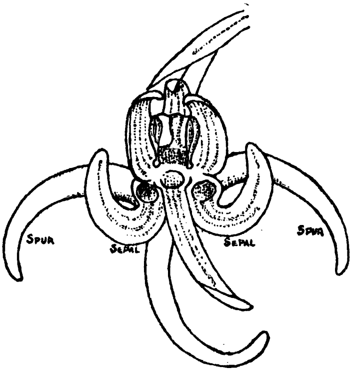

FIG. 5.—Abnormal flower of *Platanthera viridis*, with three spurs. After HEMSLEY.

In 1906 there was discovered in the county of Dorset, in England, a solitary plant of *Platanthera viridis*, the flower of which was remarkable for the possession of three spurs (*fig. 5*), one under the lip in the normal position, and one on each of the lateral sepals.[5] The extraordinary spurs entirely resembled the normal one. The general conformation of the flower was very nearly that of the species, though slight modifications were observable throughout.

The conditions of the occurrence make it highly probable that we have here the offspring of normal parents, rather than one member of a long series of gradually deviating forms; for in a botanically often- and well-explored country a race of deviants undergoing a gradual evolution from the typical condition of the species could hardly have escaped observation. It is necessary to suppose that the change of floral structure, in the line of descent embodied in this individual, supervened suddenly. The supernumerary spurs came into existence fully formed. They are not, however, new structures, except when regarded as sepallary appendages, and their origin morphogenetically and historically considered is easily discovered. The spur elaborated and perfected by the usual evolutionary processes—whatever the "usual" processes may be—as an appendage of the lip, has in a moment been transferred in full character to parts which heretofore have not been concerned—namely, to the sepals.

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[5] HEMSLEY, W. B., Journ. Linn. Soc. 38:3. 1907.

The principle is not new in biology. More than a century ago it began to be observed that when a part of such an animal as a worm is cut off, a new part different from that removed, but like some other part, may grow from the cut surface.[6] BONNET believed that there are special germs for the development of the various organs; as head-germs and tail-germs. From his experiments he made certain inductions concerning the distribution of these germs. LOEB[7] has investigated the conditions under which substitutions for lost parts may be induced, this process being regarded by him as essentially different from regeneration and deserving the distinct name heteromorphosis. LOEB also discovered that in some cases heteromorphosis can be produced without any organ being cut off, or any wound being inflicted upon the animal. Other investigators have dealt with the matter on experimental lines, especially with reference to the physiology of the process. WEISMANN has independently argued the translocation of characters from segment to segment in normal evolution of some insect larvae. He uses the word heterotopia in this connection.[8] BATESON, who appears to have discovered the principle in an original way in his study of variation, gave it the name homoeosis.[9] He describes cases in several phyla; for example,

[6] BONNET, CH., Oeuvres d'histoire naturelle et de philosophie 1:191, 215; 3: 247. 1779.

[7] LOEB, J., Studies in general physiology 115, 191, 627. 1905.

[8] The evolution theory (transl. by THOMPSON) 1:365, 367.

[9] Materials for the study of variation 85. 1894.

in Arthropoda the development of the extremity of a sawfly's antenna in the form of a foot; and in Vertebrata, the not uncommon anomalous presence upon the under side of turbots, etc., of the pigment and the tubercles proper to the upper side.

An interesting case in animals, which has lately come to my notice, is furnished by a crab, the claw being modified as shown in *fig. 6*. The superfluous claw, developed upon the normal dactyl, repeats in detail the style of the larger claw, as regards the general form and even the teeth.[10] The formation is believed not to be congenital, but to result from a wound to the normal claw near the time of moulting.

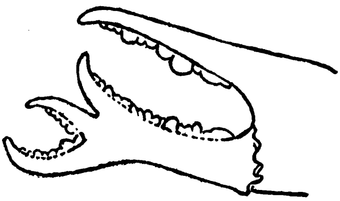

FIG. 6.—Crab claw, showing homoeosis.

The presence of the principle in animal development greatly enhances the interest which the botanical student of morphogenesis must entertain with respect to homoeosis.

In plants the transposition of organs has frequently been described in teratological works; but the phenomena of this class have been confused with those of a different nature, and the larger relations of homoeotic formations have not been recognized by teratologists. MASTERS devotes a short chapter to the subject, under the caption heterotaxy[11]—an expression which, as used by him, seems only in part to cover the ideas I am here endeavoring to formulate. MASTERS' chapter is a miscellany of teratological facts which will not go conveniently into any other chapter of his compendium. His term metamorphy[12] is too general for the present purpose, being employed

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[10] Photograph in St. Nicholas Magazine **25**:177. 1907. The specimen is in my possession. A number of similar anomalies have been described by W. FAXON, Bull. Mus. Comp. Zoöl. Harv. Coll. **8**:257. 1881; by F. H. HERRICK in "The American lobster," Bull. U. S. Fish Com. 1895, p. 145, *pl. 47;* and by other writers of whose work a summmary appears in BATESON'S *Materials*. These authors do not specifically recognize the homoeotic nature of the anomaly.

[11] Vegetable teratology 156. 1869.

[12] It will be remembered that GOETHE employed the word metamorphosis in a different sense. SACHS, again, has a definition: "Metamorphosis is the varied development of members of the same morphological significance resulting from their adaptation to definite functions."—SACHS, Text-book of botany, tr. by BENNETT & DYER (1875), 131.

"to distinguish cases where the ordinary course of development has been perverted or changed" (p. 241). This author's *Vegetable teratology*, while it is a rich storehouse of facts for the study of homoeosis, is—as might be expected from the period of its publication—entirely wanting in illuminating discussion and appreciation of relations to the problem of organic evolution such as are to be found in BATESON. The latter author recognizes the presence of homoeosis in plants.[13] SACHS distinguished clearly between atavistic formations and those which are merely translocational. His explanation of the aberrations now being considered would indeed give a degree of literality to the expression *morphic translocation*, since he attributes them to changes in sap movement, with disordered nourishment and abnormal distribution of the formative stuffs.[14] PENZIG'S perception of the real nature of the anomalies now under discussion is clear.[15]

Modes of homoeosis in plants

In the vegetable kingdom homoeosis has many interesting phases, some of which I may indicate. The facts being superabundant, it is well to begin to categorize them, not for mere convenience, but in order that new and possibly suggestive points of view may be won.

1. *The translocation of characters may be acropetal.*

Everyone recalls numerous instances where details of the foliage leaves—toothing, texture, hairing, etc.—have appeared in the floral leaves. A case of acropetal translocation is that of the corolla fringe, peculiar to *Gentiana crinita*, from its normal site to the summit of the carpels.[16] A remarkable transposition has more than once been noted, of the secretory hairs (tentacles) of Drosera foliage to the sepals, petals, and even interior of the carpels.[17]

2. *The transference may be basipetal.*

Petaloid and sepaloid characters—color, texture, outline—not infrequently appear in the involucre, and sometimes the effects reach even the foliage. The most remarkable case that has come to my

[13] BATESON, *op. cit.* 111, 570.

[14] Stoff und Form der Pflanzenorgane, §3. Arbeiten Bot. Inst. Würzburg 2:452–488. 1882; also Gesam. Abhandl. Planzenphysiologie Bd. 2:1159–1231. 1893.

[15] Pflanzen-Teratologie 2:335, 489, etc. 1890–1894.

[16] LEAVITT, Rhodora 7:14. 1905.

[17] Rhodora, *l. c.;* PLANCHON, Ann. Sci. Nat. Bot. III. 9:84, 86. *pls. 5, 6.* 1848.

notice occurs in a hybrid of the saffron (*Crocus sativus*). Stigmatic characters in this plant have wandered so far that not only the anthers and floral bracts, but also the foliage leaves are sometimes surmounted by portions of clearly characterized stigma, furnished with papillae; and even the sheaths below the leaves are tinged with saffron color.[18]

3. *Translocation may be lateral.*

Peloria, whether regular or irregular, illustrates this form of homoeosis. In the well-known *Uropedium Lindenii* (*Selenipedium caudatum*, Orchidaceae) the form of the remarkably long pendent petals invades the labellum, entirely subduing the saccate character of that member and converting the strongly zygomorphic into an actinomorphic corolla.[19] Contrariwise, the irregular member may impose its form upon the remainder of the corolla, as in the well-known peloric *Linaria vulgaris*.

4. *The invasion of migrating characters may be partial in any degree.*

The curious modifications of the pistil and its contents in abnormal *Drosera intermedia* illustrate this truth in several different ways.[20] As vegetative influences begin to evince their presence in the flower, the first modification of the gynoecium is an elongation of the ovary, especially its lower part. The carpels, while still concrescent, ovuliferous, and terminated above by the usual stigmatic apparatus, in a slight degree respond to the influx of foreign morphogenetic forces by the lengthening of their basal portions, corresponding to the petioles of foliage leaves: the carpels sensibly approach a petiolate condition. In flowers yet more affected the carpels separate in various degrees, finally falling apart altogether; their bases become elongated to form true petioles; the blades become more and more complanate and spathulate; the ovules after suffering a series of changes are finally replaced by tentacles; and the styles and stigmas, still retained even when the carpel-foliage-leaves spread horizontally from the center of the flower in rosette fashion, lose much of their rightful character. Thus is the gynoecium transformed step by step into a whorl of leaves. The metamorphosis of each part of the carpel is marked by the same flexibility and miscibility of characters which pertains to the whole gynoecium. In ovaries affected by the anomaly, but not yet resolved into separate carpellary leaves, ovules become stalked, the integuments may compose a small cup from the edge of which a few tentacles arise, or may be converted into minute modified discoid or concave leaf-blades bearing numerous minute tentacles. Between these blades, representing many characters of the radical leaves of the plant, and apparently perfect ovules, many stages of gradation have been observed. Similarly the stigmas and styles, in the most aberrant carpels, combine with their own characters the structure of marginal tentacles.

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[18] CHAPELLIER, P., Journ. Royal Hort. Soc. **24**:277. 1900.

[19] LINDEN, L., Pescat. *pl. 3;* REICHB. F., Xen. Orch. 1:*pl. 15*.

[20] PLANCHON, *l. c.* 86.

The accompanying *fig.* 7 represents advancing petaloid modification of the calyx of *Ranunculus bulbosus*. The normal sepal *A* is green and hairy on the back, while the petal is glabrous and yellow. Sepals *B*, *C*, and *D* are progressively invaded by yellowness and glabrousness (and doubtless by other corolla characters), until in *D* all that remains of sepal nature is hairiness and slight greenness in the median line of the back.

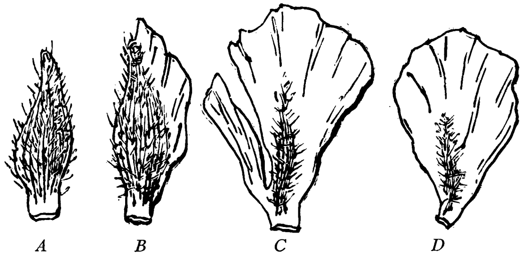

FIG. 7.—Progressive homoeosis in sepals in *Ranunculus bulbosus*. After O. AMES.

The intermediate formations described here, which are of very common occurrence in plants, are the "anamorphoses" of CELAKOVSKY.

5. *Migrating characters may transgress boundaries of homology.*

The term "homologous," applied to organs supposed to have had a common evolutionary origin, is very often vague and not rarely is practically meaningless for the reason that, while degrees of homology are infinite, the specific degree of homology in many cases cannot be known even approximately. In spite of this vagueness in the word, however, most botanists will probably agree that the ovule is in no just sense the homologue of a shoot, nor yet of a pistil, nor of a stamen, nor of a foliage leaf, nor of the droseraceous tentacle. Yet the fundaments of ovules have been observed to develop into all of these structures. LEITGEB reported[21] a *Marchantia polymorpha* in which cupules of various degrees of development (presumably with gemmae) took exactly the places of archegonia. Yet cupules and archegonia are not homologous.

6. *When against homology, the invasion may be partial in any degree.*

Without entering into details, the literature of ovular abnormality may be cited in support of this opinion.[22] Even when the imitating and imitated structures are known not to be related historically, the presence in any organ of form-giving factors derived from a different organ may merely be indicated by some faint resemblance, or may be pronounced in any degree up to the total replacement of the local member by the foreign.

A corollary of the above propositions (5 and 6) may be stated: Homology of two organs cannot be inferred on the ground alone of the replacement of the one by the other, or of the translocation of features proper to the one into the other of the organs. The existence of even a so-called "complete" series of gradations between two members does not necessarily imply the homology of the members. I think that the anamorphoses of CELAKOVSKY have not the extraordinary phylogenetic significance, as compared with other kinds of abnormality, which this author has attributed to them.

7. *In homoeosis characters may pass from one to the other of the alternating generations.*

YAMANOUCHI has recently published[23] an account of the very interesting conditions attending apogamy in *Nephrodium molle.* The apogamous prothallia bear no functional archegonia, but they proceed to initiate the sporophyte directly. A superficial cell on or near the cushion divides perpendicularly to the surface, and underlying cells divide in various directions. From the complex so originated, the sporophyte develops. The cytological history being followed throughout the critical stages, no nuclear fusions were found; and as a matter of fact the chromosomes of the sporophyte continue to be of the reduced (or x) number. Here we have a sporophytic form imposed homoeotically upon a gametophytic cell basis.

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[21] Bot. Zeit. 33:747. 1875.

[22] WIGAND, A., Grundlegung des Pflanzen-Teratologie 39. Marburg. 1850; MASTERS, *op. cit.* 186, 262–271; WYDLER, Denkschr. Regensb. Bot. Gesells. 4:77. 1859; PLANCHON, article cited; CELAKOVSKY, Bot. Zeit. 33:129–177. 1875. etc.

[23] BOT. GAZETTE 44:142. 1907; 45:289. 1908.

The contrary or aposporic case in ferns has been studied in detail by several workers. In *Athyrium Filix-foemina*, BOWER[24] found the sporangia arrested at various stages, the development being carried on by prothalloid growths which organized typical wedge-shaped cells at one or more points on their margins, while rhizoids were formed at the same time by the outgrowth of individual cells. DRUERY[25] had already observed sex-organs and even young plants arising from these prothallia. WOLLASTON[26] found in *Polystichum angulare* that the tips of pinnules were converted directly into prothallia, bearing archegonia and antheridia. In these cases a gametophytic form is imposed homoeotically upon a sporophytic cell basis (with little doubt; though the cytology, I believe, has yet to be worked out).

Entirely parallel is the production of protonemata from the setae of mosses, as observed by PRINGSHEIM[27] in Hypnum and Bryum, and by STAHL[28] in Ceratodon. LANG[29] has demonstrated the power of Anthoceros capsules to produce thalli aposporically.

The adventive structures are, of course, gametophytic, yet they arise by the prolification of sporophytic tissues.

8. *When the boundary between alternative generations is so transgressed, the invasion of extraneous characters may be partial, and both generations may be represented side by side in the same body.*

GOEBEL[30] has recently induced the formation of prothalloid growths from cut fronds of very young plants in several species of ferns. Some of the aposporous prothallia bore stomata, as well as sex organs (p. 132). LANG[31] found sporangia in various stages of

[24] Journ. Linn. Soc. **21**:360. 1886.

[25] *Ibid.* **21**:354. 1886.

[26] As reported by BOWER, *l. c.* 362.

[27] Monatsb. Akad. Wiss. Berlin, July 10, 1876.

[28] Bot. Zeit. **34**:689. 1876.

[29] Annals of Botany **15**:503. 1901.

[30] Sitzb. Bayer. Akad. Wiss. **37**:119–138. 1907.

[31] Phil. Trans. Roy. Soc. B. **190**:194. 1898.

perfection, produced in groups having a superficial resemblance to sori, upon prothallia of *Scolopendrium vulgare ramulosissimum* which had been growing for a long time without fertilization. LOWE'S cultures of *Scolopendrium vulgare* exhibited the combination of alternative generations in an interesting manner.[32] "We have here consequently a position as nearly as possible intermediate between sporophore and oophore, the sporophoric character distinctly existing in the shape of a circle of stalked fronds generated spirally from a regular axis of growth, while the oophoric character as distinctly appears in the fact that these fronds are practically stalked prothalli bearing the sexual apparatus proper to them."

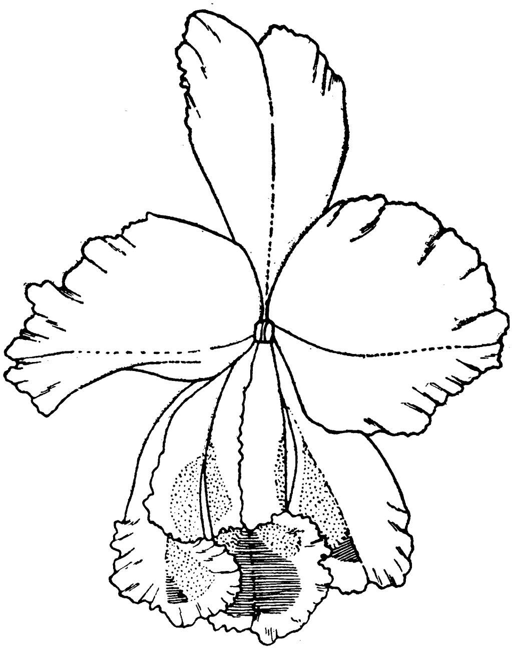

FIG. 8.—Abnormal flower of *Cattleya labiata*. After a colored drawing by O. AMES.

9. *The exact character of a homoeotic metamorphosis is often determined by the nature of the nearest normal organs.*

In many cases proximity appears to be a predominant factor. The following instance conveys more definitely the meaning of this general statement. A plant of *Cattleya labiata*, formerly grown in the greenhouse annexed to this laboratory, produced flowers uniformly exhibiting petaloid homoeosis of the calyx (*fig. 8*). The three sepals—which in normal flowers are rather narrowly lanceolate—were broadened, and their margins were crisped in imitation of the

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[32] Journ. Linn. Soc. 32:536. 1896. The quotation above is from DRUERY'S report in Mr. LOWE'S communication.

ovate crispate petals. The two lateral sepals, however, differed from the dorsal in that the inner half of each became colored like the labellum. The latter organ forms in this species, by the inflection of its margins, a loose tube, embracing the column, open distally and expanding to form the landing-stage for the pollinating insect. The floor of the tube has a broad yellow stripe, widening toward the mouth, and at the extremity replaced by a large purple or crimson-magenta patch. These colors are bounded by the pale magenta body-color of the flower. In the abnormal specimens the halves of the lateral sepals next the labellum reproduced the color-pattern of half the labellum. The halves away from the labellum were like the rest of the flower in hue. This peculiar distribution of the colors becomes interesting when an examination of the base of the perianth shows that in *Cattleya labiata* the foot of each lateral sepal is close to the foot of the labellum and overlaps it by just half—the half corresponding to the homoeotized half-limb in the abnormal flowers; while the other perianth segments stand somewhat apart from the lip. In these particolored sepals the discrimination between homoeotic and non-homoeotic areas seems to be directly related with contiguity to the "source" of the derived features.

PENZIG[33] has dwelt upon this phase of the phenomenon which we are now calling homoeosis, in his general considerations of the significance of monstrosities and in his arguments for the theory of DELPINO regarding the nature of the fertile scale in Abietineae. He was impressed, as everyone must be, with the agreement between the facts of this category and the formative-stuff theory of SACHS.

10. *A compound member may be changed in such a way that some or all of the parts exhibit the plan originally characteristic of the whole member (entropic homoeosis).*

The general plan of organization is transferred from the member as a whole to the constituent parts. Compound members may thus, by an entropism of form, suddenly become decompound. This form of homoeosis has already been illustrated in the description of the Pierson fern above. Further examples in leaves of ferns and flowering plants may be noticed here, since this variation has an interesting relation to the question of the evolutionary origin of compounding;

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[33] Pflanzen-Teratologie, *l. c.* (and elsewhere).

and besides is interesting from the purely morphogenetic point of view. The same species of variation is also to be observed occasionally in inflorescences.

A glance into two or three private and as many institutional herbaria makes it evident that entropic homoeosis is prevalent in ferns. I have found it in the ten species following, repeatedly in several of them: *Aspidium Thelypteris*, *A. spinulosum*, *Polystichum acrostichoides*, *P. angulare*, *P. Braunii*, *P. munitum*, *Asplenium thelypteroides*, *Dicksonia punctilobula*, *Polypodium vulgare*, *Osmunda cinnamomea*.

Among these species I have found the phenomenon most frequently in *Polystichum* (*Aspidium*) *acrostichoides*, in which species its operation takes some interesting turns. The fronds of *P. acrostichoides* are somewhat dimorphic, not only in the sense of being soriferous and non-soriferous, but also in the fertile and sterile fronds having slightly different general outlines. The sterile fronds have their apical pinnae non-auriculate, obtuse and oblong or elliptical to obovate. In the fertile fronds, the pinnae, again, are dimorphic, the apical ones being shorter, narrower, and abundantly soriferous. Homoeotized pinnae which I have found on various specimens represent the entire range of this dimorphism. A specimen in the herbarium of A. A. EATON, ex-herb. E. J. WINSLOW, collected in Lowman, Chemung Co., N. Y., has the two basal pinnae transformed into miniature fronds. Their length and breadth are increased, and the segmentation is quite perfect. One of them very nearly represents a fertile frond, its terminal portion being constricted and soriferous, and many of the pinnules being auriculate or toothed (*fig. 9*). Some of the pinnules,

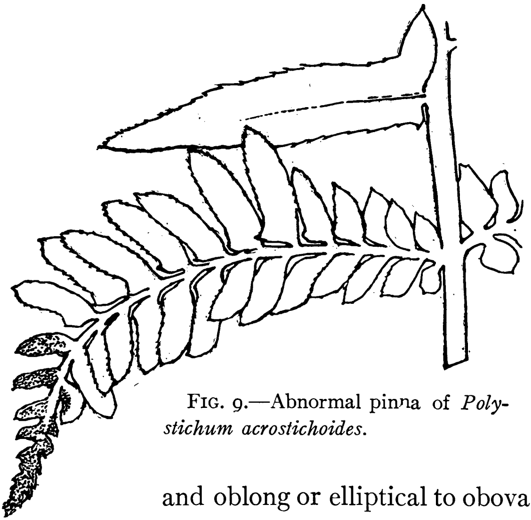

FIG. 9.—Abnormal pinna of *Polystichum acrostichoides*.

however, are of the type found toward the extremity of the infertile frond, as above described. The proximal fourth of this pinna is occupied by pinnules much shorter than the rest, so that the total width of the pinna here is about normal. This region is the part of the pinna corresponding to the stipe of the frond, and would be bare of pinnules were the frond-plan fully realized; as a matter of fact two form-forces are expressed, the pinnar, which gives a blade of proper width on either side of the mid-vein, and the frondescent, which divides the blade. In the opposite basal pinna of this specimen, segmentation is complete, but the homoeosis refers to the terminal pattern of the sterile frond.

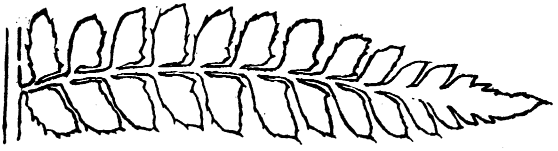

FIG. 10.—Normal pinna of *Polystichum Braunii.*

A specimen of this species in the Gray Herbarium marked "Herb. A. GRAY. Near Philadelphia, BOURGUIN," exhibits an interesting interplay of form-factors, wherein that which at first sight appears to be extreme irregularity gradually resolves itself into definite adherence to pre-existing types. Frond-plan in the pinnae is expressed by segmentation and by the character of the segments, by their increased length, and by increased width of the distal two-thirds, and in some of the lower pinnae by the absence of pinnules from the lower side of the pinnar rhachis, throughout the basal one-third or thereabouts of its length—in an "effort" to realize the petiolate condition of a frond. The segments, more or less complete, are those of the apical region of the infertile frond of the species, and the frond-form, in so far as it is realized in the pinnae, is of the infertile type. In these pinnae, the old fashion (pinnar character)

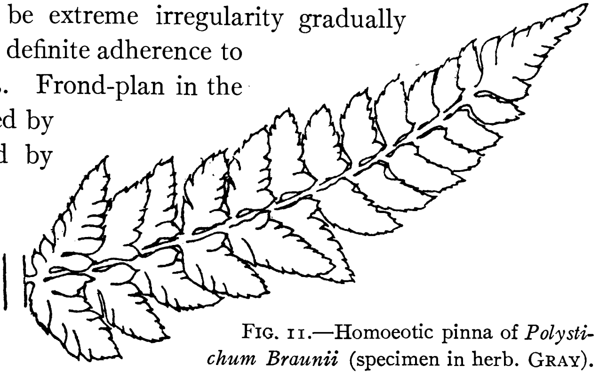

FIG. 11.—Homoeotic pinna of *Polystichum Braunii* (specimen in herb. GRAY).

is able to express itself simultaneously in the morphogenesis, by more or less successfully reducing the segmentation, by maintaining normal width in the basal region of the pinna, and by accentuating the basal segment on the upper side of the pinna, in correspondence with the large tooth or auricle which stands there in normal pinnae. The homoeotic character of the variation is unmistakable, though partial.

In a specimen from the Torrey herbarium, at the New York Botanical Garden, the frondescent pinnae of the lower section of the aberrant frond imitate an occasional trick of the species, by which soriferousness may run down the margin of the sterile region, on the tips of the pinnae. In the Torrey specimen, the lower frondlets (pinnae) are soriferous and constricted in their apical region, and the soriferousness runs down their margins on the tips of the pinnules.

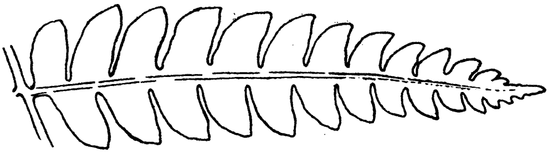

FIG. 12.—Normal pinnule of *Osmunda cinnamomea.*

Dicksonia punctilobula in the herbarium of Mr. F. G. FLOYD shows entropic homoeosis of an interesting type, inasmuch as the primary segments become frondescent in imitation, not of the adult but of the infantile, or nepionic, leaves.

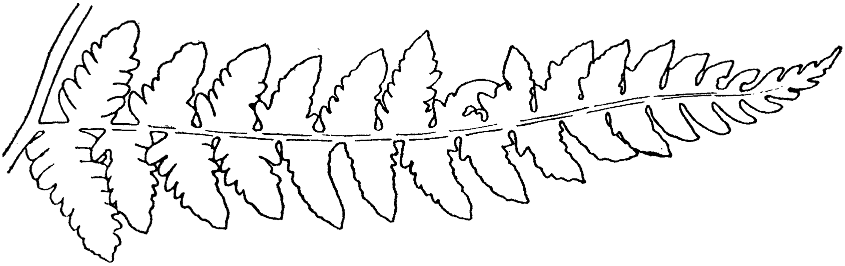

FIG. 13.—Homoeotic pinna in *Osmunda cinnamomea* (in herb. FLOYD).

Asplenium thelypteroides collected by DAVENPORT and FLOYD at Coon Hollow Brook, Milton, Mass. (hb. FLOYD), has the second and sixth pinnae frondescent (others in a less degree), the modification proceeding upon the basis of the lobing already normally present in the pinnae, and resulting in the formation of segments of a secondary rank imitating the normal primary segments; and further, in a change in spacing of the divisions, which brings the modified pinnae into conformity with the main frond-plan as regards the distance of the segments. Increased spacing, correlated with perfected divisions, in very obvious homoeosis, is also seen in *Osmunda cinnamomea* (*fig. 13*) collected by F. G. FLOYD at Mt. Desert, Me., where, according to the collector, the form is evidently hereditary, numerous modified plants covering a considerable area.[34]

Coming to flowering plants, the principle is seen in curious variations of the leaves of an Aster which Mr. C. STUART GAGER has kindly shown me. They were briefly noticed by him in *Torreya* for January, 1908. Basal laciniae have become increasingly distinct, some of them even petiolate (petiolulate); and when so, the new, or secondary, blades imitate the main blade, even down to a peculiarity of asymmetrical development.

I regard a leaf condition found by me in *Gleditsia triacanthos* as homoeotic. At any rate the variation noted is very abrupt. The character leaf of the species is simply paripinnate, the leaflets short-stalked, the blade slightly unequal at base, elliptical, obscurely serrulate or crenate, apiculate. In the leaves of vigorous running shoots (not spur shoots) I find some of the leaflets replaced by segments imitating the normal leaf in all the features specified above; the segments are, in effect, character leaves of a second order. The modified, or compound, leaflets, which are nearly twice as long as the unmodified ones, occur irregularly among the others (*fig. 14*). The condition here, essentially the same as that described for the Pierson fern, has been noticed also by GAGER (*l. c.*), one of his specimens—as also one of mine—carrying the homoeosis to the second degree, a few *pinnules* becoming perfectly compounded (as in the Whitman fern). There is no evidence, so far as I know, that the modified condition looks back to an older, normal state of division. What happens is that segments of the leaf are transformed into the likeness of something now existing—the normal, or character, leaf of

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[34] Examples of entropic homoeosis may be found in MOORE and LINDLEY, The ferns of Great Britain, etc., Nature printed. London. 1857; and in MOORE, Nature printed British ferns. London. 1859 (?).

the species. The likeness is perfect. Whether the variation here is admitted to be at the present time in each instance a fresh display of homoeosis, or is suspected of being reversionary, the abruptness of the change and the manner of its occurrence seem to me plain indications of the origin of the decompounding. It seems to me far more likely that this is entropic homoeosis, past or present, than that the complex form of the compound segments was worked into perfect likeness to the original blade slowly by natural selection.

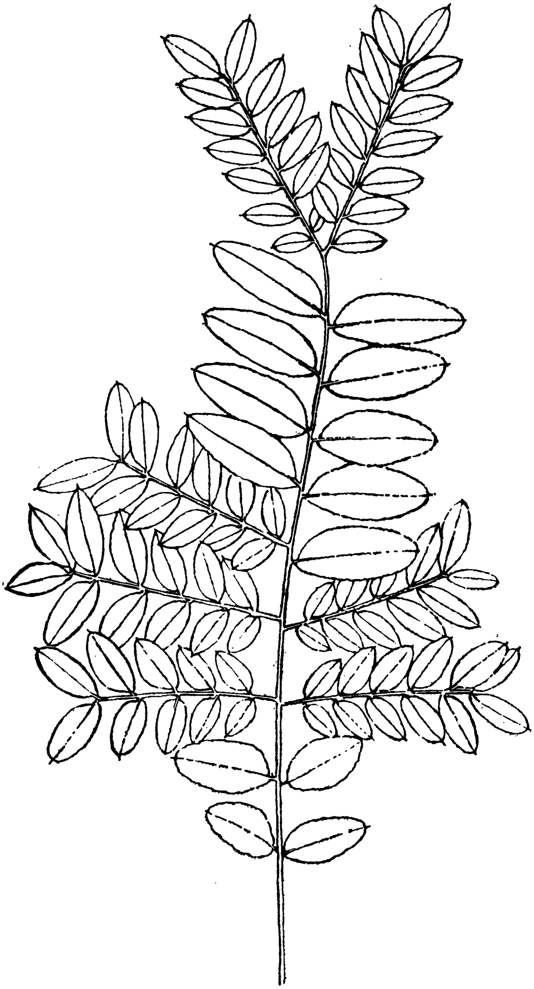

FIG. 14.—Leaf of *Gleditsia triacanthos* with seven homoeotic pinnae.

BONNET recorded a variation of the jasmine (*Jasminum officinale*) which is seen to be homoeotic in a similar way. *Fig. 15* shows the normal and variant forms side by side, as delineated by BONNET (Oeuvres **2**:363. *pl. 24*).

Inflorescences of certain marked types sometimes undergo entropic homoeosis; for example, umbels and pseudumbels. Of the former I have seen two cases, the first in *Aralia nudicaulis* (specimen in hb. N. Y. Bot. Garden, coll. by AUSTIN C. APGAR, near Lambertville, N. J., 1887). This species normally bears simple umbels at the ends of the three main branches of the scape. In APGAR'S specimen some of the florets in each umbel are replaced by long-pedicelled umbellules. That is, the form resident in the flower cluster as a whole has instantly passed into several of the parts (florets). A similar variation I have seen in *Hydrocotyle umbellata* (specimen in hb. N. Y. Bot. Garden, Jamaica, FERRY, no. 6168); and in *Daucus Carota* it was noted by CRAMER,[35] radial florets being replaced by umbels.

Two false umbels of Pelargonium in my possession are abnormal in a similar way. In each case one of the florets, eccentrically situated, has been transformed homoeotically, with the result that it rises as a pseudumbel of a secondary order from amid the flowers of the first. The subordinate flower cluster is like the chief cluster as regards centrifugal development, involucre, etc., though the flowers are fewer (8 instead of 18) and shorter-pedicelled. The secondary peduncle is articulated to the expanded summit of the primary, as are the pedicels of the flowers, and apparently would have been cast off, in event of failure to fertilize, by an absciss-layer, as with the flowers among which it stands.

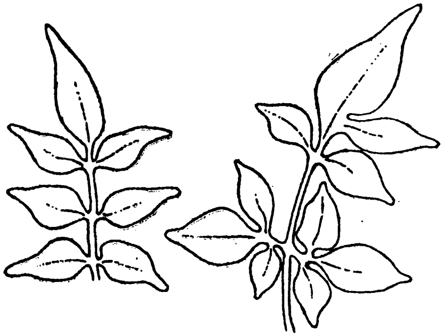

FIG. 15.—Normal leaf of jasmine (left) and a leaf with homoeotic segments (right). After BONNET.

Homoeosis and reversion

I have said that homoeosis is often confused with reversion; indeed among botanists the confusion may be said to have been habitual. The older writers having applied to homoeotic phenomena the word reversion in its ancient sense, some contemporary authors have with little reflection retained the antiquated language in expressing ideas which are altogether modern.[36]

[35] CRAMER, C., Bildungsabweichungen bei einigen wichtigeren Pflanzenfam., etc. 63. Zurich. 1864.

[36] In Rhodora 7:18, 19. 1905, I have discussed briefly the origin and use of the reversion idea as applied to plants.

In order that the real relations of the forms concerned shall be more generally recognized, one needs but to direct attention to them; argument is scarcely needed. For example, the appearance of two supernumerary spurs in *Platanthera viridis* is palpably anything but atavistic. No one at all conversant with Orchidaceae will for a moment imagine that there ever was an ancestral race of three-spurred Habenarias to which the curious Dorset plant harks back. In the above-mentioned gentian with the fringed carpel, the relation of things in evolutionary time is perfectly clear. While the carpel is an ancient, the fringe is a very recent, structure; the former was not derived from a petal, and the fringe has never until now been a carpellary appendage. When the carpel puts on the fringe, therefore, it adopts a character not to be found in its own phylogenetic line. Simply the fringe is borrowed; there is no reversion. The non-atavistic nature of the stigmatic papillae on bracts and foliage of *Crocus sativus* is equally patent. The assumption of foliage characters by carpels of Drosera is no more reversionary. The carpel of Drosera, it is safe to say, had its origin in common with that of other angiosperms, and runs back through a series of forms, none of which is a foliage leaf, to the megasporophyll of the earliest angiospermous seed-plants. Likewise the foliage leaf of Drosera is a derived structure, with characters probably more recent than the family Droseraceae even. Its peculiarities of contour and its appendages arose long subsequently to the establishment of the angiospermous, and even the droseraceous, carpel. To reach a point whence these two lines of derivation diverged, i. e., a point where the reproductive and the vegetative organs were one and the same member of the plant body, we must probably go back to the spore-bearing foliage leaf of the fernlike ancestry, far antedating the first flowering plants. The common original of the Drosera carpel and the Drosera foliage leaf was probably a kind of fern frond. The aberrant carpels in question bear no resemblance to fern fronds. They do not reproduce a form from which they are descended. They have simply taken to themselves properties of coordinate derivative members, the foliage leaves. This is so obvious that the statement would seem superflous were it not still the custom of inconsiderate writers to speak of such metamorphoses as reversions in the phylogenetic sense. The transformation is not retrograde in any except an imaginary sense; since the normal unmodified carpel is to be regarded as already "retrograde," or conservative, as compared with the tentaculiferous leaf; and the ovule as vastly more ancient than the tentacle into which it suffers change.

In peloria the morphogenetic relations are not so instantly obvious. However, the phenomenon is usually, if not always, better viewed as a homoeotic, than as an atavistic, occurrence. In notices of peloric monstrosities one often meets with the statement that these formations have a historical value. Thus, with respect to a peloric Laelio-Cattleya, MASTERS[37] suggests that here is a reversion to the earlier and simpler conformation from which the peculiar orchid structure, as we know it, has evolved. While this is true abstractly, in a merely descriptive sense—since actinomorphy doubtless preceded zygomorphy in the monocotyledonous phylum—yet it is probably untrue if we are to take it in any real phylogenetic sense, with the understanding that actinomorphy has remained latent as a hereditary character through the enormously long period of the evolution of this family from an actinomorphic condition. Regular peloria is to be considered in conjunction with the opposite change, which frequently occurs in orchids. The antithesis of the two pelorias makes it evident that we have here something besides atavism; since if either form is atavistic the other cannot be. This outcome, coupled with the fact that we have a less objectionable construction, discredits the entire idea of reversion in peloric orchids. The argument extends to other families.

Without further expatiation, it will be evident—if the standpoint of the present paper is correct—that the word reversion is a much-abused term. True reversions, except those which occur periodically in the ontogenesis, are, I suspect, rather rare. Atavism is never to be assumed off-hand in teratological cases, but it is to be admitted only when established by aid of independent proof. It should be borne in mind that *antecedents of monstrous forms are much more often to be sought in contemporary normal parts than in ancestral conditions.*

The place of these facts in botanical theory

The facts to which I am referring from a special point of view have values in botanical theory in at least three different relations:

[37] Gard. Chron. II. 31:235, 239. 1902.

first, a study of the modes or phases of homoeosis helps us to estimate at its true worth teratological evidence applied to the solution of phylogenetic problems; *secondly*, the facts seem to throw light on the method of evolution of some normal structures; *thirdly* and chiefly, the facts of homoeosis constitute, as has been already pointed out in the introductory passage, an important section of the data of morphogenetics. Let us examine these relations of the subject a little more in detail.

1. The study of homoeosis must somewhat increase the caution with which we use deviations from the normal as aids to morphological interpretation.

In the past the commonest use of abnormalities has been to make them the ground of phylogenetic inductions. The stereotyped remark of writers describing monstrous specimens has been that such aberrations "are very instructive"—an expression of faith either in the phylogenetically reversionary nature of abnormalities, or in the eternal inviolability of homology in morphogenetic sequences. Surmises from monstrosity alone were naturally more common in the days when the evolutionary story of plants was less complete than it is now, and when morphologists were driven to indirect and speculative methods. The history of this subject is voluminous; perhaps, though interesting as a study in speculation, it is more valuable for the errors which it embodies than for any content of truth; and it will not be entered into here. Some of the contentions for which teratological formations were used have been abandoned, and others have been settled by the discovery of direct evidence from comparative morphological studies of living and extinct plants. As we are enabled by extension of knowledge and maturing of opinion to understand better the relations of both normal and abnormal forms, it becomes evident that the imagined morphological significance of many abnormalities falls to *nil*. For example, we now know that the conversion of the nucellus of an ovule to a shoot, as in Aliaria and in Drosera, is wholly without phylogenetic meaning. From a study of even normal organization we are losing the belief of earlier botanists in the absolute integrity of morphological categories; and if the observations assembled in the present essay are accepted in the sense in which they are presented, it is indisputable that stages of development supposed to be concatennated in a fixed order are subject to the most violent dislocation—that a stage belonging to one morphological category may pass into another of a different category.

Abnormalities which are traceable to very ordinary features of contemporaneous organization and may be brought under the rule of homoeosis, will for the moment lose all historical force which they may ever have been thought to possess. Historical significance can be restored to them only by application of the laws (if we may so speak of the operations) of homoeosis. If homoeosis much more easily follows lines of homology, and only rarely transgresses them under very special conditions, then frequent homoeotic metamorphosis of a particular organ in a particular direction may be thought to be indicative of the derivation of the organ. But I think that the admission of homoeosis in any case is practically fatal. The method of inference then becomes too roundabout to be acceptable to modern taste. If in any case homoeotic formations agree with the results of comparative morphology, of anatomy, and of organogeny, still they add only a reflected light to the general illumination.

In writing these words I have in mind particularly the long debate over the morphological nature, or origin, of the ovuliferous scale in conifers; or so much of it as relates to malformations. Perhaps no single organ of vascular plants has afforded morphologists more matter for disputation than this scale, which has a vast literature of its own by the most eminent authorities—LINNAEUS, A. BRAUN, SCHLEIDEN, VON MOHL, EICHLER, SACHS, BAILLON, STRASBURGER, VAN TIEGHEM, DELPINO, PENZIG, MASTERS, NOLL, CELAKOVSKY, and others. The theories of these authors have been various, and based upon every conceivable consideration, not least upon abnormalities. Teratology has appealed very differently to different students—to some as supporting one doctrine, to others as favoring a different theory; to some as of great or even decisive weight, to others as having no significance at all. CELAKOVSKY, who has studied the matter most persistently, has relied upon abnormalities, and especially upon unbroken series of intermediate formations, such as those between the fertile scale as it separates into parts (at the appearance of a shoot) and the leaves (or bud scales) of the shoot. This author assumes that such gradations can exist only between homologous organs. He regards the entire composite structures found in the monstrous cones, made up of the fertile scales and the shoots which grow through them, as such intermediate formations (anamorphoses), and looks upon them as sufficiently proving the shoot-nature of the fertile scale.[38]

From the numerous clear and detailed drawings of the abnormal cones which have been published,[39] certain truths are apparent enough. First, no new organ or form of any organ, not proper to the species of today, except intermediate formations between present-day vegetative and reproductive parts, is to be found in the cones. No ancient structure, nor anything suggesting ancestral structures, nor any organ of paleobotanical aspect, makes its reappearance out of the past; there is no reversion. If the shoot in the axil of the bract, replacing the scale, were truly atavistic, we should expect that lost characters would appear in the axis and its appendages. But the shoot turns out always to be an ordinary leafy branch with the reduced foliage representing the xerophytic adaptation of the group. This shoot is not reversionary in even a barren formal and descriptive sense; for if the fertile scale represents a shoot, now reduced to two ovules and their expanded integuments, the relics of two sporophylls, and if the original development of axis and sporophylls is to be restored, we ought to have in the restoration an axis terminated by sporophylls or by ovules as representing them, since megasporophylls when reduced to a pair are terminal appendages; but this development is not realized in the abnormal cones, in which we find that the shoot arises sometimes above or below the scale, and when in the midst of it, then in the form, not of a stalk, but of a proliferation, upon which the parts of the fertile scale become basal appendages—if they are to be taken as appendages of this shoot at all.

The transformations of the cone are homoeotic. And therefore, while it is in itself not unlikely that the fertile scale represents a pair of sporophylls belonging to an axillary shoot, and while comparative morphology and anatomy may make this view even probable, the monstrous cones, it seems to me, add nothing material to the satisfaction which one may take in this solution of the conundrum.

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[38] CELAKOVSKY'S writings summarize the whole controversy (Abh. Kgl. Böhm. Gesell. Wiss. VI. **11**:1882; VII. **4**:1892; ENGLER'S Bot. Jahrb. **24**:202. 1898). More accessible may be WORSDELL'S review (Annals of Botany **14**:39. 1900), or that of COULTER and CHAMBERLAIN (Gymnosperms 69–77. 1901).

[39] E. g., CELAKOVSKY, Abh. Kgl. Böhm. Gesell. VI. **11**:1882; PARLATORE, Ann. Sci. Bot. IV. **16**:*pl. 13*. 1862; STENZEL, Nov. Act. Nat. Cur. **38**:*pls. 12–15*. 1876; VELENOVSKY, Flora **71**:*pl. 11*. 1888.

Nor is their value improved by the anamorphosis idea. To me at least the "transitions" from fertile scale to axillary shoot do not appeal with the same compulsion with which they appeal to CELAKOVSKY and some others. I can conceive the most perfect of these transitions to represent combinations of historically unrelated form-factors, reproductive on the one hand and vegetative on the other; and in the conception I find nothing incongruous with other facts of homoeosis. If there were originally no shoot in the axil of the fertile leaf (the bract) but only an ovuliferous segment (SACHS-EICHLER) or pair of lobes (DELPINO)—supposing for argument that these notions were admissible on any but teratological evidence—and if by influx of vegetative forces the cone were converted *gradatim* into an ordinary branch, with buds in the axils of the leaves; then it seems to me that we might expect to discover morphogenetic impulses toward the formation of ovuliferous segments and impulses toward bud-formation coexistent and cooperative in the same body of axillary tissue, with such a result as the monstrous cones exhibit. After reviewing the combinations of diverse formative impulses in teratological occurrences generally, I do not feel that CELAKOVSKY'S case for the preeminent value of anamorphoses is established. In comparison with other sources of suggestion the monstrous cones seem to have a minimal value. The interest and worth of CELAKOVSKY'S thoroughgoing study of the whole subject does not lie in his treatment of monstrosities.

Yet a small degree of approval for the theory which makes the scale represent a shoot bearing sporophylls might possibly be derived from the frequency with which a shoot arises in the site of the scale; and this in spite of the facts that there are irregularities and that more than one plausible reason might be given for the frequent appearance of the shoot. The latter has been found in the genera Larix, Picea, Pinus, Tsuga, Cryptomeria, Cunninghamia, Glyptostrobus, Sequoia, Taxodium, and some other genera.

I hope that it may be clear that the shoot-and-sporophyll theory is not here called in question, but only the use of teratological formations as competent evidence. The ground is taken that these formations do not remove all doubt as to the origin of the fertile scale, but on the contrary only after all doubt has been removed as to the nature of the scale, by legitimate argument from comparison of normal structures, do the monstrous formations begin to have any considerable historical significance.

2. Homoeosis has played a part—necessarily from its nature, which is essentially anarchical, a small part—in the evolution of plants. We can trace to a homoeotic origin certain established sequences in development, of which specific examples may be adduced.

(*a*) *Habenaria quinqueseta* (or *Michauxii*) of the southern states carries on vegetative reproduction by certain of its roots. At the apex of these roots, close to the *punctum vegetationis*, pointing backward in the embryonic tissues, a stem apex is organized. *Fig. 16* shows its relations to the apical regions of the root. Two leaves and a bud in the axil of one of them have already been differentiated. Subsequently to the stage here represented, the root-apex enlarges and forms at the base of the new shoot a spherical tuberoid growth evidently with storage functions.

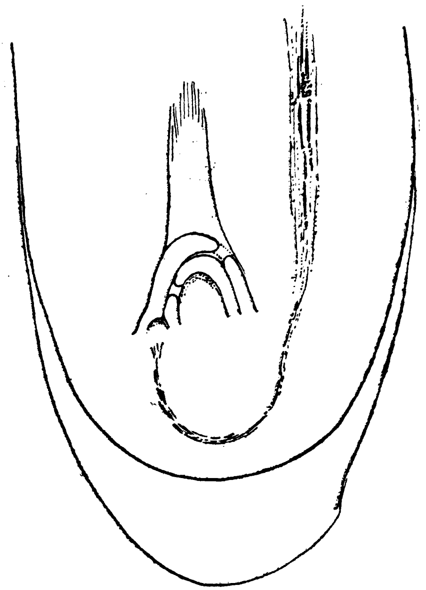

FIG. 16.—Median longitudinal section of root of *Habenaria quinqueseta*.

As to the evolution of a shoot fundament in this curious position, no one, I suppose, will imagine that the entire evolutionary history of the stem, leaf, and bud in cormophytes has been repeated in the interior of a Habenaria root. It is perfectly clear that the form-giving agencies which shape the leafy shoot in this species have been set to work upon tissues which up to a certain point have been dominated by other forces. There is nothing new except the extraordinary morphogenetic sequence. In this instance, morphic translocation has become habitual, or normal.

(*b*) In *Phyllonoma ruscifolia* of Mexico the flowers are regularly produced from the upper surface of leaves, near the apex (*fig. 17*). There is no adnation in this case, for the anatomy of the blade below the inflorescence and of the petiole shows no addition to the normal vascular structure, indicating any concrescence. Here again an abrogation of ordinary morphogenetic sequence has become fixed in the development.

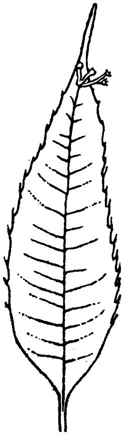

FIG. 17.—Leaf of *Phyllonoma ruscifolia.*

(*c*) The specific form of the vegetatively derived embryo in some plants must be considered homoeotic; as for example in *Opuntia vulgaris*, described and figured by GANONG.[40] At the time when fertilization should take place, the egg cell, according to GANONG'S observation, has become disorganized. The place of the normal embryo is taken by several embryos budding in from the nucellus. The noteworthy feature of these apogamous individuals is their adoption of the form of the abdicating embryo proper. Here is a homoeosis which has become established and provides a regular means of propagation for the species. A considerable number of such cases is known.

It is natural to imagine that conditions in the embryo sac determine the form of the buds and cause the homoeosis; yet it is not at all certain that such is the explanation of the assumption of form. In a case observed by myself the embryos organize outside of the sac. I refer to *Spiranthes cernua* of the meadows. The upland form of the species has a normal development. In the variety growing everywhere in rich meadows I have seen only polyembryonic seed. Having followed the development with care, I find that the embryo sac ceases to develop after a few nuclei have been formed in it, and is pushed aside by the hypertrophic inner integument. This envelope, normally composed of a few flattened cells overlying the sac, in this variety of the species early takes on a very active growth, forming a mass of cells which, as it comes to maturity, splits up into rounded bodies simulating the embryo of the genus.[41] The formation of embryos is often incomplete and growth then results in amorphous masses; but on the other hand, it is often successful, and gives such seed-contents, consisting of several well-made embryos, as that figured herewith (*fig. 18*). It is true that the form is very simple, for the normal embryo has neither suspensor nor cotyledons. But that cells of the inner integument, ordinarily forming a saccate one-celled layer, with not the remotest resemblance to an embryo, should so much change their habits, and in the transformation should select the fashion, though simple, of embryos, is sufficiently singular. I look upon the process as homoeotic in its nature.

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[40] BOT. GAZETTE **25**:221. 1898.

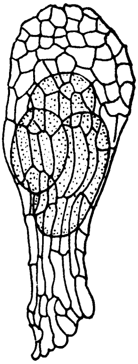

FIG. 18.—Seed of *Spiranthes cernua* (lowland form).

The formation of embryos here is quite independent of pollination, as I have proved by carefully castrated and guarded flowers—an ecologically important item for a species blooming so late in the season. The biological significance of the process, indeed, is—if I may digress for a moment—that the plant by this means combines the certainty of issue which pertains to vegetative methods of reproduction, with the swiftness of dispersal and range of dissemination secured by the seed apparatus. This is doubtless the combination of favorable circumstances which has secured the wide adoption of apogamy in Compositae also. In *Spiranthes cernua*, homoeosis supervening in the integument has doubtless contributed to the abundance of the species in suitable soils from Massachusetts and Ontario to Georgia (I know not how much beyond these limits, which bound my search for the polyembryonic condition).

(*d*) Still more remarkable is the transference, discovered by

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[41] Rhodora **2**:227. 1900.

Rosenberg,[42] of a whole series of characters from the megaspore and embryo sac to a somatic cell in *Hieracium flagellare.* The embryo sac is sometimes formed normally, but in the greatest number of cases this structure aborts. A neighboring cell, which may be situated in the epidermis of the nucellus or in the chalazal region or in the integument, takes upon itself the function of a megaspore, though without reduction of the chromosome number. This cell enlarges to form an embryo sac. Its nucleus divides as that of the megaspore would do; egg apparatus and antipodals are formed; and even polar nuclei fuse to form an endosperm nucleus. The gametophyte is thus reproduced, after the failure of the proper organ to construct it, by a cell of the sporophytic generation. And this homoeotic process is habitual, hereditary, and established in the species.

If Hegelmaier's observations upon *Lycopodium Selago* are correct,[43] we may attribute the formation of the gemmae of this species and its near allies to a homoeotic origin. The gemmae—detachable shoots—arise in exactly the position of leaves, from which in their earliest stages they are indistinguishable.

The form of homoeosis most often entering into the diversification of species of plants is apparently that which has above been called entropic. Abscission of leaflets has already been discussed in this connection. Another seemingly homoeotic feature of compound leaves is found in their stipels. An examination of stipels in a considerable number of groups—as in Xanthoxylum, Staphylea, Enscaphis, Turpinia, Robinia, Bradburya, Desmodium, Galactia, Dolicholus, Vigna, Amorpha, Sambucus—strongly suggests that the stipels have arisen as echoes of the antecedent structures, stipules, when in the evolution of the leaf suitable conditions have been established. They occur in plants possessing stipules, and with little doubt already in possession of them before leaf-compounding set in; they are generally useless, as far as one can see; when they have a visible use it is the same as that of the stipules, in a much weakened degree; they follow punctiliously the greatly varying character of the stipules—being large, stout, and thorny; slender, terete, rigid, and sharp-pointed; long, weak, and membranaceous; small or evanescent or flattened and glandular-capitate, etc.—in the different groups; they occur in situations much resembling the situations occupied by the stipules. All of these facts suggest that the compounding of the leaf with organization of partial leaf-stalks, in evolution, has been the occasion for the production of stipels homoeotically.

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[42] Bot. Tidsskrift **28**:150. 1907.

[43] Bot. Zeit. **30**:841. 1872.

Moreover, we may well suspect that in many cases decompounding of the blade has followed upon compounding from the same general cause; the partial blades borrowing the compounding tendency from the parent blade, the whole leaf thus becoming by a single step decompound. The circumstance that the ground-plan of the whole leaf is repeated in miniature in the several parts, in a vast number of decompound leaves of both phanerogams and ferns, and the occurrence of the corresponding type of homoeosis as individual variation in both divisions, lend a color of probability to this conception. Decompounding, on this hypothesis, would have no initial relation to utility, and would not be a product of natural selection.

To consider this matter a little further with respect to ferns: If the variation which we find so frequently in ferns has been the basis of evolutionary advance in complexity of the frond, we should be able to discover in the decompound-leaved species certain relations which would necessarily follow from such an evolution. We should certainly find the ground-plan repeated in the segments. We should expect to find, further, that the historically earlier and simpler conditions would be retained in youthful leaves; and that these youthful leaves would be matched by the segments of the fully developed fronds of the mature plant. Both these expectations are met in many species. Ferns on every hand illustrate the first. Of the second, a single example will be enough to direct attention to the facts which are easily observable. In *fig. 19* are reproduced a youthful frond of *Polystichum angulare proliferum*, and a pinna from an adult leaf. In *Asplenium Filix-foemina* we have a depauperate variety, var. *exile* D. C. Eaton, the mature frond of which is very precisely matched by the pinna of the frond of the typical form.[44]

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[44] See EATON'S Ferns of North America *pl. 76*.

Further, if entropic homoeosis has given us decompounding widely in ferns, we shall expect to find species so related to each other that some represent the original types and others the homoeotic derivatives. We shall look for, first, the simply pinnate types; secondly, types in which the pinnae match the fronds of type *1;* and perhaps thirdly, a type in which the fundamental plan is worked out in the pinnules. If the simple type has two modes, as above described for *Polystichum acrostichoides*, we may expect to find either or both represented in the more complex patterns.

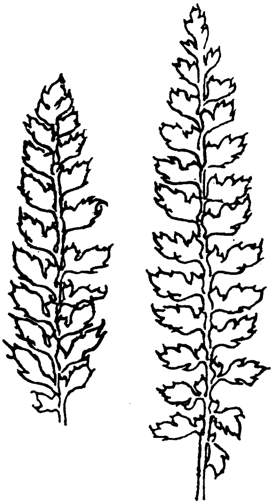

FIG. 19.—Youthful frond and pinna from adult frond of *Polystichum angulare proliferum.*

Anyone having access to a collection of Polystichum may see this projected scheme filled out by existent species. First we have the simply pinnate forms, such as *P. acrostichoides*, *P. munitum*, *P. lonchitis;* in which we have two frond patterns, *1a* being the fashion with more or less oblong, non-auriculate pinnae, probably historically earlier, seen in a pical regions of sterile fronds; and *2b* being the characteristic plan, the pinnae falcate-auriculate. Then we find many species with pinnae frondescent in facsimile of pattern *1a* or *1b;* as *P. californicum* (*1a*) and *P. Lemmonii* (*1a*), *P. aculeatum* (*1b*), and *P. Braunii* (*fig. 10, 1b*, sometimes *1a*); and others, a considerable number of species. Finally, frondescence of the second degree is well represented in *P. angulare tripinnatum* (*1a*, in the ultimate segments). In *P. scopulinum* the (supposititious) homoeosis is incomplete, the proximal region of the pinnae alone being segmented (*1a*), the distal merely lobed.

We find species so much alike (except that one of two is simply pinnate, the other decompound) that one appears to have been derived directly from the other by entropic homoeosis; as the West Indian *P. viviparum* (decompound *1a*) from *P. triangulum* (compound). In Europe *P. aculeatum* and *P. lonchitis* stand in a similar relation to each other; the slight differences—apart from homoeosis—are such as might be expected to arise in specific isolation.

In homoeosis a character or a system of organization which has been evolved in one part of the body is transferred, ready made, to another part. The great mass of instances are of the class called teratological. By this designation we mean, substantially, that they are suddenly appearing deviations from the customary structure. "Monstrosities" in general have the special value that their chronology is oftentimes ascertainable; we know that such and such identical plants have arisen in the midst of normal relatives. They exhibit, as has been said, discontinuous or saltatory variation. That homoeotic monstrosities typify homoeosis in general, as a saltation phenomenon, may be inferred from the very nature of the process. When, therefore, we discover homoeosis at work in normal evolution, diversifying lines of descent, we are able to augment the steadily increasing collection of evidences for discontinuity in the origin of specific differences.

Homoeotic changes may thus be classed with mutational phenomena. But grouping them with the mutations exhibited by the Oenotheras rests only upon some such negative property as that homoeotic transformations fall outside of any law of the evolution of characters by natural selection. It seems unlikely that the two classes of alterations have anything further in common. Mutation proper seems to result from some qualitative change in the inheritable substratum of organization; while in homoeosis no new qualities are introduced, but only old characters are recombined, or characters are evoked in a new sequence in development. Homoeotic transformations are, indeed, found among the instances of mutation which DE VRIES uses in *Die Mutationstheorie* (for example, peloric *Linaria vulgaris*). They have to be classified under this author's *degressive Artbildung* (p. 461, B 2, a). Yet their inclusion in a classificatory scheme of variations under mutation seems to rest on purely formal and abstract descriptive resemblances.

3. The idea of homoeosis unites for descriptive purposes a great number of facts of ontogenesis which, even though they may not

at the present juncture point a way to the correct mechanical explanation of development, possess in this connection a considerable prospective value. An adequate theory of ontogenesis must take these facts into account.

Their value lies in their exceptionality. Homoeotic occurrences are fundamentally antithetic to our usual conception of the method of development. The most general and fundamental of our notions of a mechanically autonomic evolution from egg to adult, is that of a series of states (A, B, C, D . . . . X, Y, Z), so related that each one necessarily serves as the stage upon which the next state arises. Every one of the several states seems to be the needful condition for the appearance of the next following. This is the primary conception of ontogenesis derived from ordinary experience. It is contradicted by homoeotic formations. We see the usual sequence violated at some point, and a state (as X) arising upon a state (as D) from which it does not normally arise, and from which we have supposed that, in the very nature of the process, it cannot arise directly.

In homoeosis, then, we have a new ontogenetic phenomenon. Herein lies its worth; for every datum of a new sort adds to the materials for a true theory of development, and increases the chances of our finding a clew to the right construction and combination of the materials.

Although the times are doubtless not ripe for the appearance of an adequate theory, and further attempts in this direction may be profitless for the present, yet almost universally there has been felt the desirability of biomechanical hypotheses going behind the bare facts of development. We have had from DARWIN, NÄGELI, DEVRIES, SACHS, ROUX, WEISMANN, DRIESCH, and others a series of more or less elaborate attempts at an explanation. I think that anyone at all familiar with this line of biologic endeavor will recognize the progress in substantial knowledge effected under the influence of such speculations—even though they deal with gemmules, pangens, micellae, biophores, and less concrete "organizations," far beyond the range of the microscope. And it is entirely possible that some of the suggestions already offered may be germinal points from which a verifiable system will develop.

The most persistent attempt at a solution has been made by WEIS-

MANN, who has erected a theory of the nucleocentric type, wherein the control of development is made to reside within the several cells, and specifically within the chromatic matters of the nucleus. Nuclear divisions are conceived as being of two types; namely, (1) equating, in which the germ-plasm is conserved in its integrity, all characters of the mother nucleus being shared equally by the daughter nuclei; and (2) differentiating division, in which the daughter nuclei receive from the parent nucleus unlike assortments of character-giving bodies. All the determinants, capable of giving form to the whole organism, being present in the nucleus of the egg, differentiation is concomitant with an orderly distribution of the governing bodies, effected in the successive nuclear divisions, each different part of the body ultimately receiving its proper kind of determinant.

In view of present limitations of our knowledge, the theory of WEISMANN is a highly speculative system, and as such has been freely modified to meet emergencies arising from the discovery of new facts. There is perhaps little forensic satisfaction to be gained from argument under these conditions. Yet it is undoubted that the the proposal of this hypothesis has prompted investigations leading to interesting discoveries. And even as a means of throwing observations into some sort of order, any such theoretic scheme has its use. It seems to me, therefore, well worth while to consider all kinds of facts of ontogenesis in the light of this and other generalizations in morphogenetics. The facts of regeneration have thus been arrayed with relation to the Roux-Weismann hypothesis. Regenerative phenomena take on, in consequence, some new aspects, and the whole subject gains in spirit. A tentative relation is established between regeneration and morphogenetical theory in general.

The effect upon the Roux-Weismann theory has been the introduction of a fundamental modification. For the power of reproducing lost parts, so widely possessed by animals, and in some degree by plants, is not accounted for by the Roux-Weismann idea in its most unequivocal form. To allow for this faculty, the cells, even of differentiated tissues, instead of being deprived of all elements except those expressed in the usual form of these tissues, are now allowed to retain sets of determinants sufficient for purposes of regeneration. This auxiliary equipment is, however, tightly stowed. Under ordinary conditions only the *differential* determinants are free to influence the development of the cell and its activities, the regenerative or reserve determinants being held strictly under restraint until they are called for, to reconstruct lost members.

Homoeosis has a similar influence with regeneration upon the Roux-Weismann idea; and perhaps a more destructive influence. For while the facts are quite as striking, they are very much more varied and abundant. And if the vast array of data, the existence of which has been suggested in the present article, is added to the evidence from regeneration, the necessity for providing full reserve-funds of determinants in differentiated parts is much increased. Many parts of the body—this statement is made especially with reference to plants—are able to produce almost any other part. We are probably warranted in postulating a pangenerative capacity for every vital member. We know that a single epidermal cell of the leaf in Begonia may originate a complete plant. Indications are not wanting that single living plant cells in general intrinsically possess the same power, ordinarily latent, its exercise inhibited by circumstances. If each cell possesses a complete character-fund, the characters capable of being severally activated upon motion of factors external to the cell, does not the necessity for imaging special individualized determinants disappear? Can we not as well think that differences in cells and forms of organs spring from the nature of the molecule of the form-giving substance (probably chromatin), this substance being the seat of morphogenetic powers ready to be evoked and responding variously to the diverse conditions in which, in the course of development, the substance finds itself placed? Obviously, in proportion as all cells of an organism are made to appear equipotential in a morphogenetic sense, does the need of assuming the existence of different kinds of form-giving substance diminish.

Whatever be the basis assumed for an explanation of the micro-evolution which we call ontogenesis—whether the existence of special form-controlling bodies, or the general properties of the organic molecules, or organ-forming stuffs capable of diffusion, or some other basis—the abrupt diversion of formative currents and transformation of members into others of usually dissimilar origin, the frequent appearance of forms in locations not expected in the ordinary sequence of development, and the potentiality of all parts in each part, indicated by the general phenomenon which we have been calling homoeosis, will need to be provided for in our ultimate theory of development.

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